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A TOOTH-BEARING MAXILLA REFERABLE TO *LYCORHINUS ANGUSTIDENS* HAUGHTON, 1924 (DINOSAURIA, ORNITHISCHIA)

By

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(With 7 figures)

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ABSTRACT

The taxonomic status of the genera *Lycorhinus* and *Heterodontosaurus*, and the various specimens referred to them, is in an unsatisfactory state, due to incomplete preparation and description of otherwise good material, a tendency to diagnose specimens rather than species, and a lack of understanding of the anatomy and functioning of the teeth. A new tooth-bearing maxilla is described in detail, and both it and the type and only specimen of *Lanasaurus scalpridens* Gow, 1975, are referred to *Lycorhinus angustidens* Haughton, 1924, which is also restudied and reinterpreted here. Although detailed descriptions of the dentition of *Heterodontosaurus tucki* Crompton & Charig, 1962, have not yet appeared, *L. angustidens* and *H. tucki* are readily distinguishable on postcanine tooth morphology, angle of wear facets, and pattern of occlusion. Authors have ranked these differently specialized contemporary species as primitive and advanced; this practice may be questioned.

CONTENTS

INTRODUCTION

In 1984 James Kitching and the author collected a tooth-bearing left maxilla of an Early Jurassic ornithischian dinosaur. Any new material of these rare and incompletely known animals is to be welcomed. As the specimen was studied it became apparent that it is a larger specimen of the species *Lanasaurus scalpridens* Gow, 1975, and that both are referable to *Lycorhinus angustidens* Haughton, 1924. Impressions were accordingly made of the type of *L. angustidens*, thus enabling a detailed study of the three specimens. The study shows that *Lycorhinus angustidens* differs from *Heterodontosaurus tucki* Crompton & Charig, 1962. Most described material resides comfortably in one or the other of these species, with the exception of *Lycorhinus consors* Thulborn, 1974. The much discussed specimen UCL A100 (Thulborn 1970) was probably correctly identified as *L. angustidens*; it cannot be grouped with *L. consors* as *Abrictosaurus* Hopson, 1975. The intention of this paper is to refrain as far as possible from discussing the work of previous authors but rather to concentrate on presenting new facts and inferences.

The following abbreviations are used to indicate the repositories of the material studied:

BP — Bernard Price Institute
SAM — South African Museum
UCL — University College, London.

THE NEW MAXILLA

Locality

The farm Bamboeskloof, Lady Grey: 30°45′S 27°12′E, map reference Floukraal 3027CC.

This locality is less than 15 km from two *Heterodontosaurus tucki* localities in the Herschel district (Crompton & Charig 1962; Santa Luca *et al.* 1976) and approximately 130 km from the type locality (Mount Fletcher) of *Lycorhinus angustidens* Haughton, 1924. *Lanasaurus scalpridens* Gow, 1975, was found about 250 km to the north (Golden Gate Highlands National Park). (See outcrop and locality map in Kitching & Raath 1984, fig. 1.)

Material

The specimen (BP/1/5253) had been exposed to the elements for some time prior to collection, with the result that the more delicate dorsal and anterior projections of the maxilla are missing. The cutting edges of the teeth are also damaged and two crowns are missing.

Preparation

Only a little mechanical preparation was necessary. This was followed by treatment with thioglycolic acid, but this was discontinued as some damage to the specimen became evident; this was in any case only cosmetic preparation. Useful X-ray plates were made from the specimen.

Description (Figs 1, 3–5)

In occlusal view (Fig. 5) three important features are seen: the pit for reception of the lower canine, the deep cheek region, and the pronounced curvature of the dental arcade. The dentition is fully developed and well worn, indicating that this was a mature individual. There are 14 functional teeth and a rudimentary 15th. The teeth invite several descriptive analogies; they are broadest linguolabially and closely packed like a row of kernels on a maize cob. (The teeth of *Lanasaurus scalpridens* are broadest mesiodistally, but this difference can be attributed to age—compare Fig. 6.) Lingually and labially the crowns stand out from the roots (as evident in the photographs and indicated by dotted lines in Fig. 1). This swelling of the crowns is reciprocated by swellings of the roots at the mesial and distal 'gum lines' (for example see tooth 5). The final analogy is that the teeth have a symmetrical cold-chisel shape with a constant included angle of about 75° between wear facets and labial crown surfaces. (The narrower teeth of *L. scalpridens* have an included angle of 45°. Thus, although the angle is age dependent, it is worth stressing for comparison with *Heterodontosaurus* that the new maxilla belonged to a mature individual.) This included angle is a useful means of comparison as it is not affected by damage to the cutting edge of the crown and it eliminates subjective reference to vertical and horizontal axes.

More anterior teeth have taller crowns, whereas mesiodistal crown width increases towards the back of the tooth row. The crowns have mesial and distal ridges on their lingual and labial surfaces separated by grooves from the main body of the crown; the distal ridges and grooves are more pronounced; on the lingual surface grooves persist for some time as wear proceeds and are thus important for assessing ages of teeth.

In the following text teeth are referred to by numerals for convenience. Part of a wear facet is preserved on 2 but this tooth and 3 have lost much of the crown tips; 5 is lightly worn with part of the posterior groove still present; 6 is younger than its neighbours, being very little worn; 7 appears to have complex wear, but the two small basal facets were probably induced by trapped food rather than direct tooth on tooth contact (this is an old tooth); 8 is also well worn. Here one begins to see the pattern that persists from this point posteriorly, whereby adjacent wear facets on successive teeth were formed by a lower tooth in staggered occlusion. This pattern becomes very clear when the teeth are viewed normal to the wear facets (Fig. 1B—lines on the left in the figure separate inferred lower teeth). Steps between adjacent teeth in this occlusal view immediately show up young teeth and correlate with those teeth (in Fig. 1C) that retain traces of a posterior groove (notably 6 and 9; 12 is more worn). Tooth 9 is lightly worn, 10 is heavily worn with some blurring between the two main facets, possibly the result of polishing by food but also possibly the remnant of an earlier facet (as argued for *Lycorhinus angustidens*—see below). Tooth 11 has a well-developed pair of wear facets. Tooth 12, though a moderately young tooth (presence of posterior groove), is complicated, as its anterior facet is actually paired—the result of being opposed by two successive lower teeth. This tooth also has a large food polish facet. Teeth 13 and 14 are well worn (retention of the posterior groove on the latter possibly due to delayed eruption of a suitable antagonist). The rudimentary tooth 15 indicates that this is a fully elaborated, mature dentition.

Teeth 6, 9 and 12 form a series of increasing age and are clearly younger than the two teeth that follow each. Replacement thus proceeds from back to

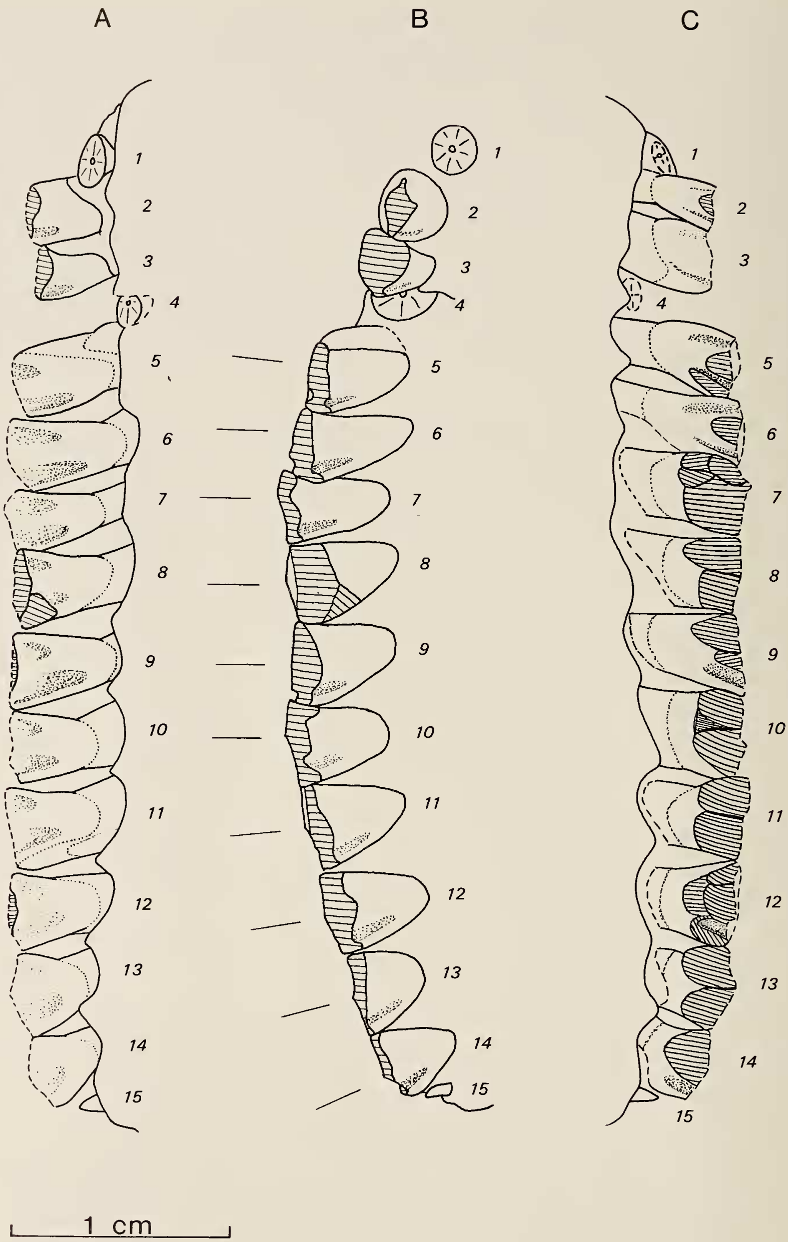

Fig. 1. *Lycorhinus angustidens*, BP/1/5253, left maxillary dentition. A. Labial view. B. Viewed normal to the wear facets. C. Lingual view. Note: In A and B hatching denotes broken areas. In C wear facets are hatched. Lines to the left of B indicated where lower teeth met each other.

front in the row. This is the same as the pattern described by Gow (1975) for *Lanasaurus scalpridens* (Fig. 6) and similar to that by Hopson (1975) for *Lycorhinus angusticeps* but with a slightly modified interpretation (see below).

This has interesting implications. In the described dentition, teeth within triplets are arranged in order of increasing age from front to back, but after two more replacements a stage would be reached when this order would be reversed, and it was just such a stage that pertained in the maxilla that opposed the type dentary of *Lycorhinus*, as demonstrated below. X-rays of the specimen reveal root canals filled with dense haematite; these show that only a very thin layer of maxillary bone roofs the deep tooth sockets: the canal fillings terminate at the alveolar border. In the tooth sequence 6 to 13, root-canal fillings are present for all except tooth 7—this is probably a quirk of preservation as 7 should be the last in the series 13–10–7 to be replaced. X-rays of *L. scalpridens* reveal a full complement of roots. Although these X-rays show no signs of replacement activity, this is not a firm indication that replacement had ceased. X-raying is a non-destructive technique that should be routinely applied and improved.

Lycorhinus angustidens

Figs 2, 3, 7

The specimen, SAM–3606, has been well described by Hopson (1975, 1980) but was re-examined for this study owing to the possibility (now considered confirmed) that the new maxilla belongs to the same species. In order to take impressions, the specimen was thoroughly wet and the excess water removed with compressed air; a fabric-reinforced latex impression was then made, the first layer being of a very watery consistency. Three impressions were taken and all are equally good. The impressions were coated with a fine film of sublimating ammonium chloride, and it is these that were studied and photographed.

The present interpretation differs slightly but significantly from that of Hopson (1980). The first point, which has not been stressed previously, is the marked curvature of the postcanine tooth row. When the canine is oriented with its cutting edges in a sagittal plane, the postcanine row curves back strongly labiad. (The new maxilla matches this curvature. The best way to see this is to orientate the photographs of the occlusal view with the first three teeth in the sagittal plane.)

The canine bears serrations on both edges (four per millimetre) as illustrated by Hopson (1980, fig. 1). However, most of the distal edge of the tooth is missing.

Postcanine 1 bears a small mesial cusplet and above it the margin of the crown is damaged (i.e. there may have been other cusplets). The posterior half of the labial surface of the crown is damaged and this looks like wear, as the damaged area has a sharp but smooth enamel edge (the worn area is covered with matrix grains firmly adhering to the dentine surface).

Postcanine 2 has a worn occlusal edge to the crown; it also has a mesiolabial wear facet almost certainly formed when the erupted tooth made contact with the opposing upper tooth that had earlier been responsible for making the facet on 1M—the first indication of a staggered pattern of occlusion of upper and lower cheek teeth, which is argued in detail later. The condition of the labio-distal surface of 2 is not clear due to adherent matrix, but it does seem confluent with the anterior facet on 3.

Postcanine 3 has a small distal cusplet high on the crown. There is some conchoidal fracture of the dentine at the tip of the crown but this does not mask two distinct wear facets dipping slightly away from each other. Tooth 4 is very similar though more worn and better preserved. Hopson's (1980) interpretation of tooth 5, i.e. one major wear facet and a small polished area, is accepted. Hopson interpreted tooth 6 in the same way but the larger lower facet is in fact in perfect contiguity with the anterior facet on tooth 7, thus demonstrating the presence of an upper tooth in overlapping occlusion with 6 and 7.

Postcanine 7 is an old tooth; its posterior wear facet bears a wide, deep, smoothly rounded groove. This groove must have been formed by a step between adjacent edges of occluding upper teeth at different stages of wear. A small facet is present on the mesial edge of 8. By tilting the specimen it is possible to see that this facet lies on the same arc as the distal facet on 7—these facets are thus attributable to the same upper tooth. The author is not convinced that there is sufficient evidence for the same situation pertaining between 8 and 9, but agrees with Hopson (1980) that it seems likely. The large wear facets on 8 and 9 have deliberately been left unhatched in Figure 2 because these teeth

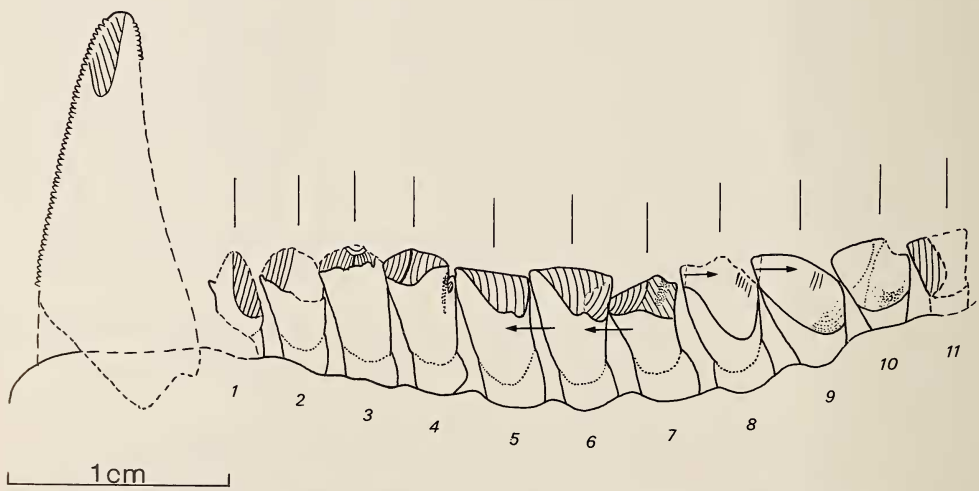

Fig. 2. *Lycorhinus angustidens*, SAM–3606. Impression of left dentary teeth. Hatching indicates wear facets but has been deliberately omitted from teeth 8, 9 and 10. Teeth 8 and 9 bear striations, 9 and 10 have heels shown by shading, and 10 bears a raised ridge with the same orientation as the striations on 8 and 9. Wear facet on canine is on the lingual surface of the tooth.

bear patches of striations indicating direction of bite. These striations are helpful to understanding the bite, which is seen to have a posteriad component. It is important to note that the striations have the same orientation as the ridge on tooth 10 discussed below. That such striations are rare suggests a degree of imprecision in the bite such that occluding surfaces are continuously roughly polished. Teeth 9 and 10 have heels worn into the base of their facets. The present interpretation of 10 and 11 differs from Hopson's but is made with the benefit of the hindsight afforded by the new maxilla. Tooth 10 has a raised ridge between facets, such as would result if the edges of occluding uppers did not quite meet.

The preserved portion of the 11th tooth was clearly part of a perfectly normal full-sized tooth; it is faceted and is raised labiad of 10, and it was thus opposed by the successor to the tooth responsible for the posterior facet on 10. It is suggested that the differences in wear facet orientation that Hopson (1980) recorded (supposedly increasingly horizontal with age) are illusory, as witness the continuity of facets on 7 with those of its neighbours. Indeed tooth 4 seemingly has the most nearly horizontal wear facets, but is less worn than tooth 5, which apparently has more oblique facets. This specimen represents a mature animal of a species characterized by very oblique wear facets. Three more teeth could have been present in the living dentary (see Fig. 3).

This dentition contains ample evidence of a staggered occlusal arrangement between upper and lower teeth. In Figure 2 vertical lines above teeth indicate where upper teeth would meet each other. Some of the most interesting and instructive lower teeth are those that at first sight apparently do not conform to this staggered pattern. The best place to begin is with tooth 6: here it is seen that a second wear facet has started to encroach on a previously existing single facet—the new facet would continue to enlarge and migrate forward as indicated by the arrow. One can postulate that exactly the same thing would happen in time to tooth 5. Teeth 8 and 9 differ in that they have very well-developed

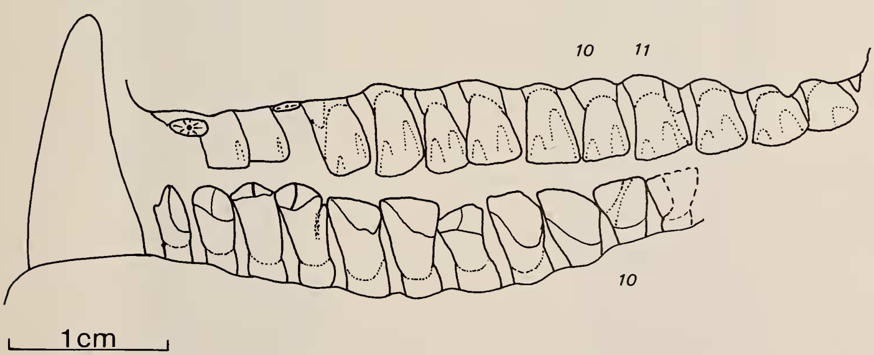

Fig. 3. *Lycorhinus angustidens*. Composite drawing of BP/1/5253 and SAM–3606. The specimens fit rather well and give an indication of the degree of incompleteness of the dentary tooth row. For reasons explained in the text, wear facets cannot be directly compared.

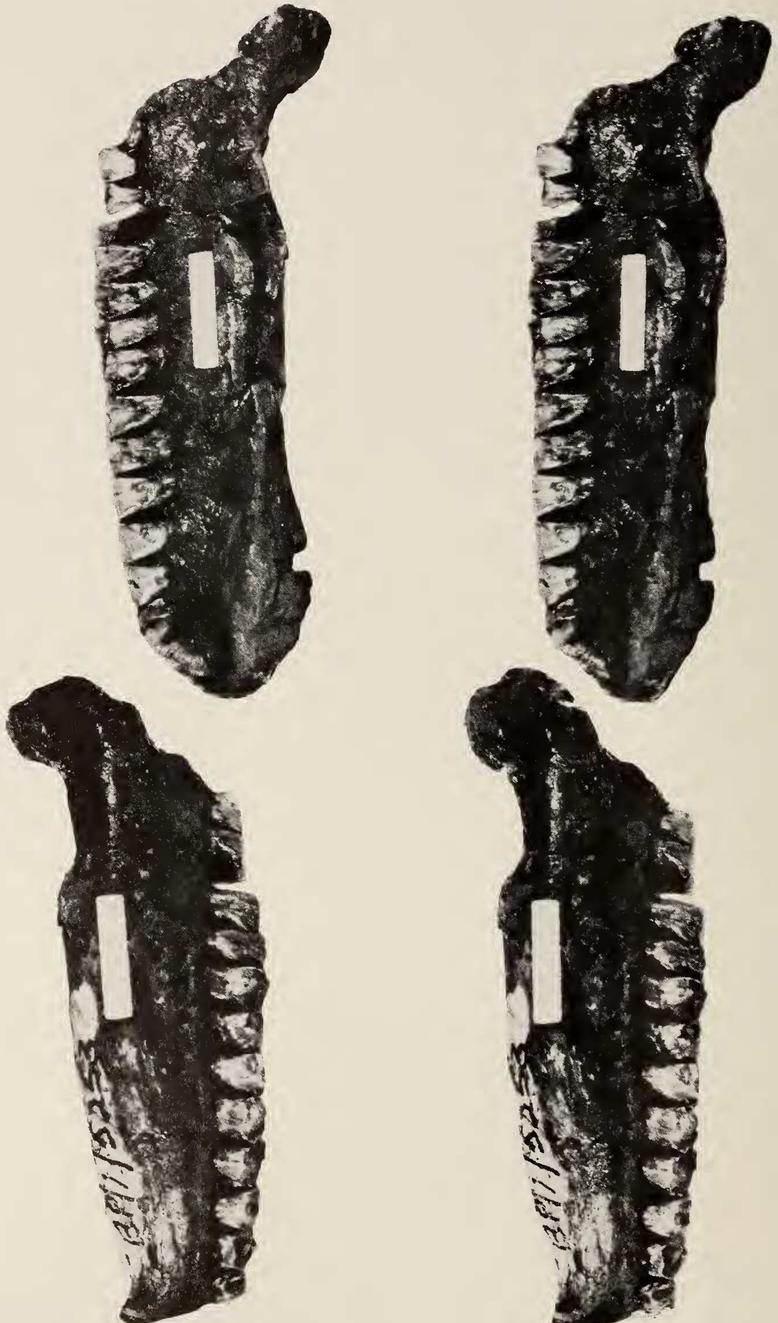

Fig. 4. *Lycorhinus angustidens*, BP/1/5253. Above. Labial view. Below. Lingual view. Scale bar = 1 cm.

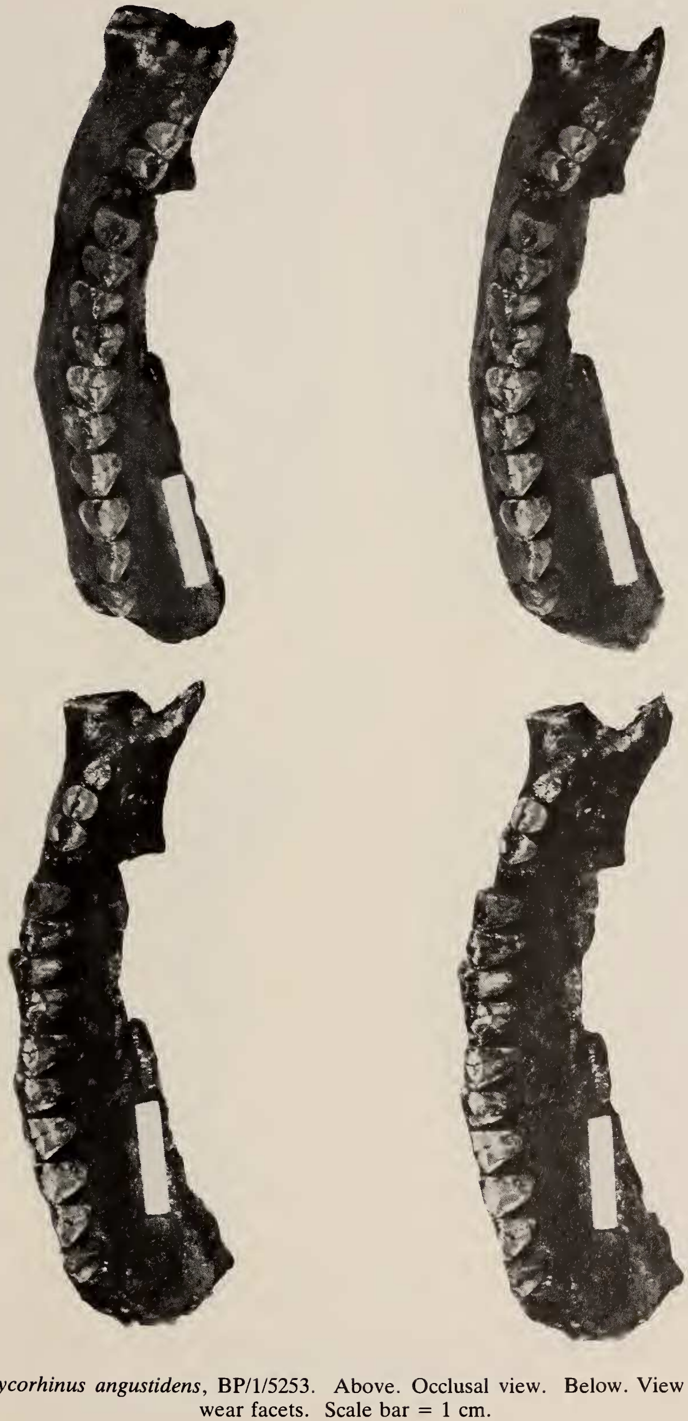

Fig. 5. *Lycorhinus angustidens*, BP/1/5253. Above. Occlusal view. Below. View normal to wear facets. Scale bar = 1 cm.

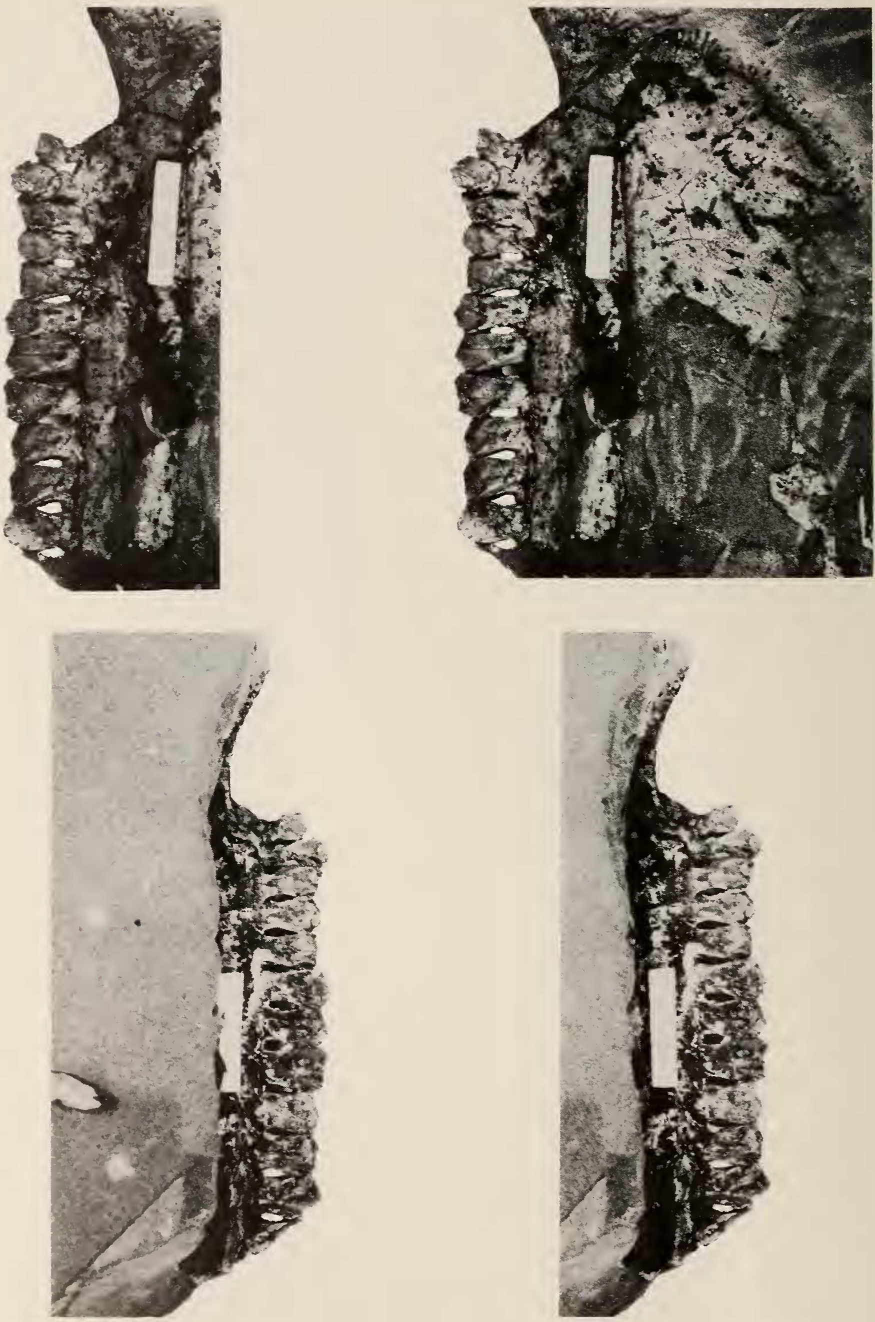

Fig. 6. *Lycorhinus angustidens* (*Lanasaurus scalpridens*), BP/1/4244. Above. Labial view. Below. Lingual view. Scale bar = 1 cm.

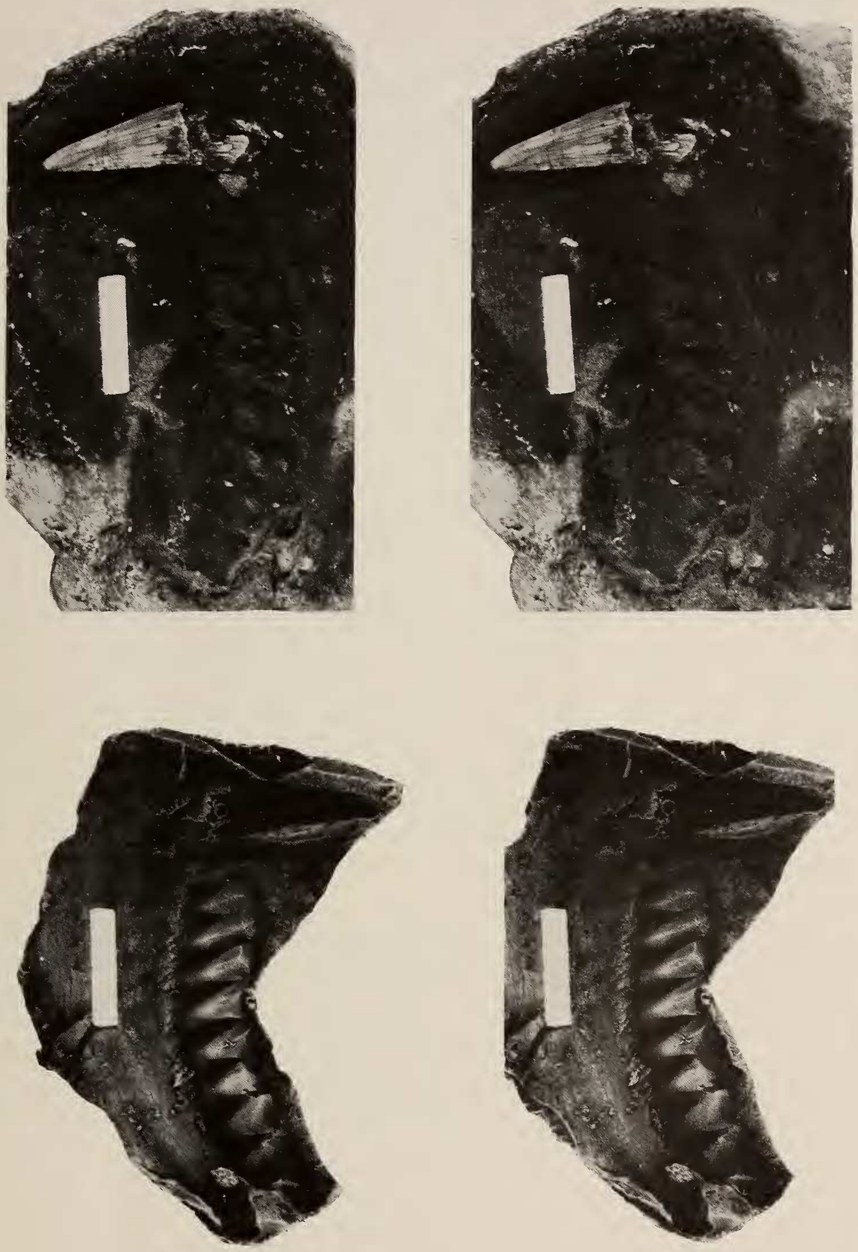

Fig. 7. *Lycorhinus angustidens*, SAM–3606. Original above. Positive impression below. Scale bar = 1 cm.

single facets, and incipient facets on their anterior edges. These latter facets would migrate posteriad in time until these teeth reached the condition seen in tooth 10, which has two distinct but very well-worn facets. After this the tooth would be shed. The difference in direction of facet migration has little to do with position in the tooth row, but seems rather to be related to the extent of wear of the teeth. From the above, the following sequence can be inferred.

(a) A single wear facet forms fairly symmetrically over the labial surface of the crown of a dentary tooth (as previously noted by Hopson such a facet is concave—the opposing upper teeth would be well worn and would present a convex surface). This is not apparent from Figure 1B and perceptions of facet curves change as the specimen is rotated about its longitudinal axis. At its best development each of a pair of facets on adjacent teeth is concave, hence a convexity is formed where they meet. This is seen in the occlusal stereophotograph (Fig. 5) between teeth 7 and 8, and 10 and 11.

(b) A second facet forms posteriorly when a new upper tooth comes into occlusion. This facet migrates forward and eventually dominates the crown as the tooth anterior to it is shed (this facet extends further down the crown—quite obviously this must be so).

(c) As a new tooth comes into occlusion in the anterior position, a third facet forms, this time on the anterior edge of the tooth, and this migrates backwards to result in the condition seen on tooth 10. At this stage the tooth would be replaced.

This interpretation highlights, and is itself supported by, the pattern of triplets in the *Lycorhinus* jaw. Arranged from youngest to oldest, these are 5, 6 and 7, and 8, 9 and 10. This interpretation differs from that of Hopson (1975, 1980), who proposed the following triplets: 4, 5 and 6, and 7, 8 and 9. Turning to the anterior teeth, it appears that 4 is more worn than 3, but both have two facets, whereas 2 has a single (first wear stage) facet; thus these teeth conform to the pattern of triplets proposed here.

We now have the interesting situation where both maxilla and dentary bear triplets of teeth that consistently range in age from front to back. For the lower jaw one can demonstrate that each triplet would require to be opposed by a battery of teeth in which the reverse situation pertained. To do this we can look at the hypothetical maxillary (M) triplet 6, 7 and 8 that occluded with dentary (D) teeth 6, 7, 8 and 9 at the time the bearer of the *Lycorhinus* type died. Tooth M6 was well ground in, M7 had only recently made contact with D8, whereas M8 may just have made contact with D9. We can also look at D9, 10 and 11: the oldest tooth in the next maxillary series should be M9—that fits; M10 should be mature but not as old as M9 and again this is borne out by the wear facet on D11. All this makes eminently good sense, as, if occluding teeth were to erupt together, the amount of attrition would presumably be greater and the teeth would wear faster.

The pattern of wear on the teeth in the new maxilla has been frozen at a different stage in the cycle, which makes it look different and more difficult to